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Estimation of combining ability through line × tester in Rice (*Oryza sativa* L.)

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Abstract
The present investigation was undertaken to estimate combining ability and gene action for yield and quality traits in rice (*Oryza sativa* L.) using a line × tester mating design comprising three lines, eight testers and 24 F_1 hybrids. Significant genetic variability was observed for most of the traits studied. The GCA/SCA variance ratio was less than unity for all traits except protein content, indicating the predominance of non-additive gene action, while additive gene action governed protein content. Among the lines, DRR DHAN-48 was identified as a good general combiner for productive tillers per plant, grain yield per plant, harvest index and protein content, whereas IET-31950 was superior for grains per panicle, straw yield per plant, kernel length, kernel breadth, 100 grain weight and amylose content. Among testers, IET-31929 was identified as a good specific combiner for productive tillers per plant, grain yield per plant and kernel breadth, GNR-9 for number of grains per panicle, protein content and amylose content, IET-31937 for days to 50 per cent flowering, number of grains per panicle and straw yield per plant, GR-23 for number of grains per panicle, straw yield per plant and GR-15 for 100 grains weight. SCA estimates indicated that the cross, DRR DHAN-48 × DRR DHAN-45 was identified as a superior cross combination for productive tillers per plant, number of grains per panicle, grain yield per plant and straw yield per plant, IET-31950 × GR-23 for productive tillers per plant, number of grains per panicle, grain yield per plant and straw yield per plant and NVSR-6640 × IET-31929 for number of grains per panicle, straw yield per plant, kernel length and protein content. Among the quality traits, IET-31950 × GR-26 was identified as a superior cross combination for kernel length, while IET-31950 × GNR-9, NVSR-6640 × IET-31929, DRR DHAN-48 × IET-31938, NVSR-6640 × IET-31937, DRR DHAN-48 × GR-15 and NVSR-6640 × GR-26 exhibited desirable significant sca effects for protein content, indicating their potential for developing superior rice hybrids.

Keywords: Rice, line × tester, combining ability, yield and quality traits

Introduction
Rice (*Oryza sativa* L.) is a self-pollinated cereal crop belonging to the family Poaceae with a chromosome number of 2n = 24. The rice flower consists of a centrally located pistil enclosed by six stamens, and the crop serves as the principal source of nourishment for a large segment of the Asian population (Huang *et al*., 2012) [13]. The genus Oryza comprises 24 species, of which only O. sativa (Asian rice) and O. glaberrima (African rice) have been domesticated. O. sativa, which originated in South and East Asia, is broadly divided into the indica and japonica subspecies, while molecular characterization has further classified it into five major groups, namely indica, aus, tropical japonica, temperate japonica and aromatic rice (Garris *et al*., 2005) [12]. Rice is the staple food for nearly 90 per cent of the Asian population and contributes approximately 700 calories per day to about three billion people worldwide (Juliano, 1985; Vlachos and Arvanitoyannis, 2008) [14, 32]. The grain contains 70–80 per cent starch, around seven per cent protein primarily in the form of oryzenin, which possesses high digestibility (93%), a biological value of 74 per cent and a protein efficiency ratio ranging from 2.02 to 2.04. It also contains about three per cent fat along with B-complex vitamins and essential mineral nutrients (Eggum, 1969; Fresco, 2005; Oko *et al*., 2012) [10, 25]. Globally, during 2024–25, rice was cultivated on approximately 168 million hectares with a total production of 542.03 million metric tonnes of milled rice (Anonymous, 2025a). In India, rice production during the *kharif* and *rabi* seasons of 2024 [31]–25 reached 122.77 and 27.41 million metric tonnes from cultivated areas of 41.50 and 8.03 million hectares, respectively (Anonymous, 2025b). In Gujarat, the crop occupied about 1.015 million hectares, producing 2.44 million tonnes with an average productivity of 2410 kg/ha (Anonymous, 2025c).

Rice contributes more than one-fifth of the total global dietary calorie intake; however, it is nutritionally inadequate to satisfy the daily requirement of essential micronutrients, making biofortification an effective strategy for improving grain nutritional quality (Juliano, 1992; Visakh *et al*., 2024) [15, 31]. The enhancement of iron (Fe) and zinc (Zn) concentrations in rice grains through conventional breeding and modern biotechnological approaches provide a sustainable means of combating micronutrient malnutrition, which remains a major public health concern worldwide (Bhavya *et al*., 2023) [8].

Combining ability study helps the breeder in selecting the parents and breeding methods to be employed to improve a particular trait, as it provides the information on the genetic nature of the traits. Combining ability analysis provides instructions for determining the relative breeding worth of parental material at an early stage. GCA is attributed to additive (fixable) gene action and SCA caused by non-additive gene action, however, is non-fixable and may be due to by dominance, additive × dominance, dominance × dominance or higher order gene interaction. The primary basis for starting the hybrid programme is the presence of non-additive genotypic variance. The ratio of GCA to SCA variance provides an estimate of the predominance of additive gene effects or the non-additive gene effects.

Materials and methods

Plant material: Eleven diverse genotypes including DRR DHAN-48, NVSR-6640, IET-31950, GR-15, GR-23, GR-26, GNR-9, DRR DHAN-45, IET-31937, IET-31929 and IET-31938 were used for the estimation of combining ability in rice for yield related traits. Out of these 3 genotypes were used as lines *viz*., DRR DHAN-48, NVSR-6640 and IET-31950 and 8 were used as testers *viz*., GR-15, GR-23, GR-26, GNR-9, DRR DHAN-45, IET-31937, IET-31929 and IET-31938 for developing 24 crosses in a line × tester mating design.

Field evaluation of single cross F_1 hybrids: Twenty four F_1 hybrids were developed and evaluated along with 11 parents in Randomized Block Design in three replications during *Kharif*-2025. The investigation was carried out at Main Rice Research Centre, NAU, Navsari. Navsari is situated at coastal region of South Gujarat in the Agro-climatic zone of heavy rainfall. Geographically, it is situated at 20°-37' N latitude and 72°-54' E longitude with an altitude of 11.98 meters above the mean sea level. Each entry was planted in single row consists 20 plants with a spacing 20 cm x 15 cm.

Data analysis: At maturity, data was recorded using five competitive plants which were randomly selected for all the observations like, plant height (cm), productive tillers per plant, panicle length (cm), grains per panicle, grain yield per plant (g), straw yield per plant (g), harvest index (%), kernel length (mm), kernel breadth (mm), L/B ratio, 100 grain weight (g), protein content (%) and amylose content (%). But days to 50 % flowering was recorded on plot basis. The mean value of observed plants was subjected to statistical analysis. The analysis of variance was performed to test the difference among parents and hybrids for all 14 characters. The variation among the hybrids was partitioned further into sources attributed to general and specific combining ability components in accordance with the procedure suggested by Kempthorne (1957) [18].

Result and discussion

The analysis of variance in Table 1 revealed that hybrids were found highly significant for all characters except plant height and panicle length, which indicated sufficient variability present among hybrids. The differences between parents were highly significant for all the characters except plant height, panicle length, harvest index and amylose content. Among parents, mean sum of squares due to females were significant for all characters except days to 50% flowering, plant height, panicle length, grains per panicle, straw yield per plant, harvest index and amylose content and mean sum of squares due to males were significant for all characters except plant height, panicle length and amylose content indicating the presence of wide genetic variability among the parents for most of the characters. The mean sum of squares due to males *vs* females were highly significant for characters days to 50% flowering, productive tillers per plant, grains per panicle, grain yield per plant, straw yield per plant, kernel length, kernel breadth, 100 grain weight and protein content which indicated that female and male parents differed significantly for these characters.

The analysis of variance for combining ability was carried out for fourteen characters and the mean sum of squares are presented in Table 2. The hybrid variation was partitioned into lines, testers and line × tester interactions. The mean sum of squares due to lines were significant for productive tillers per plant, grain yield per plant, harvest index, 100 grain weight and protein content, whereas non-significant effects were observed for days to 50 per cent flowering, plant height, panicle length, grains per panicle, straw yield per plant, kernel length, kernel breadth, L/B ratio and amylose content. The mean sum of squares due to testers was non-significant for all the characters studied. The line × tester interaction effects were significant for days to 50 per cent flowering, productive tillers per plant, grains per panicle, grain yield per plant, straw yield per plant, harvest index, kernel length, kernel breadth, L/B ratio, 100 grain weight, protein content and amylose content, whereas plant height and panicle length exhibited non-significant interaction effect.

Table 1: Analysis of variance of experimental design for yield and yield related characters

SOV	df	Days to 50 % flowering	Plant height	Productive tillers per plant	Panicle length	Grains per panicle	Grain yield per plant	Straw yield per plant
Replications	2	10.78	222.66	0.33	12.17	8.857	12.08	30.85
Genotypes	34	65.07**	124.22	3.38**	4.03	1,208.07**	62.19**	335.40**
Parents	10	110.78**	127.25	2.20**	4.99	403.81**	36.02**	375.24**
Males	7	66.42**	142.48	1.03**	4.88	420.27**	15.45*	398.83**
Females	2	32.11	87.91	4.21**	6.37	149.60	30.52*	9.04
Males *vs* Females	1	578.69**	99.32	6.40**	2.96	797.05**	190.96**	942.54**
Hybrids	23	44.18**	126.71	4.04**	3.62	1,502.69**	76.12**	324.58**
Parent *vs* Hybrid	1	88.46*	36.77	0.04	4.02	2,474.29**	3.47	185.83*
Error	68	13.29	138.32	0.22	4.08	58.01	6.55	32.34

Table 1: Conti

SOV	df	Harvest index	Kernel length	Kernel breadth	L/B ratio	100 grains weight	Protein content	Amylose content
Replications	2	10.79	0.01	0.00	0.01	0.01	0.00	0.70
Genotypes	34	49.45**	0.46**	0.07**	0.13**	0.18**	10.76**	5.92**
Parents	10	36.96	0.57**	0.03**	0.14**	0.09**	16.95**	3.13
Males	7	46.89**	0.16*	0.03*	0.10**	0.05*	17.26**	3.27
Females	2	16.48	1.06**	0.04**	0.27**	0.18**	19.69**	4.19
Males *vs* Females	1	8.40	2.43**	0.07**	0.10	0.19**	9.31**	-0.00
Hybrids	23	55.208**	0.43**	0.09**	0.12**	0.22**	7.61**	7.247**
Parent *vs* Hybrid	1	41.93	0.00	0.08**	0.24**	0.11*	21.21**	3.53
Error	68	10.91	0.05	0.01	0.03	0.02	0.07	1.95

* and ** indicates significance at 5 % and 1 % levels of probability, respectively.

For days to 50 per cent flowering, negative gca and sca effects are desirable as they indicate earliness. Among the testers, IET-31937 recorded highest significant negative gca effect (-4.64) and identified as a good general combiner for earliness. The remaining testers and lines exhibited either positive or non-significant negative gca effects and were therefore considered less desirable for this trait. The estimates of sca effect revealed that none of the cross combinations exhibited significant negative sca effect for days to 50 per cent flowering. None of the hybrids were considered a good cross combination for earliness based on sca effect. Similar results were documented by Santhiya *et al.* (2024) [27] for both gca and sca effects, while Dianga *et al.* (2020), Garkoti and Pandey (2022) and Balasubramanian and Vennila (2024) [6, 9, 11] reported similar gca effect for the concerned trait.

For plant height, negative gca and sca effects are generally desirable as they contribute to the development of semi-dwarf plant types. None of the parents exhibited significant gca effect for plant height. Similarly, the estimates of sca effect revealed that none of the hybrids exhibited significant desirable sca effect for plant height. These findings are in agreement with the results of Bhatti *et al.* (2015), Kargbo *et al.* (2019), Nanditha *et al.* (2021) and Garkoti and Pandey (2022) [7, 11, 17, 23] for gca effect.

Table 2: Analysis of variance for combining ability and variance components for different characters

Source of variation	df	Days to 50 % flowering	Plant height	Productive tillers per plant	Panicle length	Grains per panicle	Grain yield per plant	Straw yield per plant
Replication	2	6.00	227.89	0.75	8.34	10.12	18.05	51.12
Hybrids	23	44.18**	126.72	4.04**	3.624	1502.69**	76.12**	324.58**
Line effect	2	29.29	359.27	14.26*	2.47	1092.50	276.02*	276.53
Tester effect	7	59.54	100.27	2.07	6.35	2113.32	49.03	178.31
Line × Tester effect	14	38.62**	106.72	3.56**	2.42	1255.96**	61.11**	404.58**
Error	46	11.29	127.96	0.23	4.13	46.15	7.60	26.08
Variance components								
		0.75	9.63	0.58	-0.06	43.60	11.18	10.43
		5.36	-3.07	0.20	0.24	229.68	4.60	16.91
		9.11	-7.08	1.11	-0.57	403.26	17.83	126.16
		2.00	6.17	0.48	0.01	94.35	9.38	12.20
		9.11	-7.08	1.11	-0.57	403.26	17.83	126.16
		0.22	-0.87	0.43	-0.03	0.23	0.34	0.09

Table 2: Conti.

Source of variation	df	Harvest index	Kernel length	Kernel breadth	L/B ratio	100 grains weight	Protein content	Amylose content
Replication	2	37.04*	0.01	0.00	0.01	0.02	0.03	0.06
Hybrids	23	55.20**	0.43**	0.09**	0.12**	0.21**	7.61**	7.24**
Line effect	2	310.30**	0.93	0.08	0.06	0.68*	69.47**	10.51
Tester effect	7	15.89	0.10	0.07	0.14	0.19	1.95	6.44
Line × Tester effect	14	38.42**	0.52**	0.10**	0.13**	0.16**	1.60**	7.18**
Error	46	10.36	0.07	0.01	0.03	0.02	0.05	1.87
Variance components								
		12.49	0.03	0.00	0.00	0.02	2.89	0.36
		0.61	0.00	0.00	0.01	0.01	0.21	0.50
		9.35	0.15	0.03	0.03	0.04	0.51	1.76
		9.25	0.02	0.00	0.00	0.02	2.16	0.40
		9.35	0.15	0.03	0.03	0.04	0.51	1.76
		0.98	0.17	0.14	0.12	0.52	4.17	0.22

* and ** indicates significance at 5 % and 1 % levels of probability, respectively.

For productive tillers per plant, positive gca and sca effects are desirable. Among the lines, DRR DHAN-48 (0.83) exhibited a significant positive gca effect and was identified as a good general combiner for this trait, Among the testers, IET-31929 (0.87) exhibited a significant positive gca effect and was identified as a good general combiner for increasing the number of productive tillers per plant. With regard to sca effect, three hybrids exhibited significant positive sca effect for productive tillers per plant. The cross, DHAN-48 × DRR DHAN-45 (1.93) recorded highest positive sca effect and was identified as superior specific combiners for increasing the number of productive tillers per plant. Present results are in close agreement with earlier reports of several workers like Nanditha *et al.* (2021), Garkoti and Pandey (2022), Kushal *et al.* (2023) and Aruna *et al.* (2024) [5, 11, 20, 23].

For panicle length, positive gca and sca effects are desirable. The estimates of gca effect revealed that none of the lines exhibited significant positive gca effect for panicle length. Similarly, none of the testers showed significant positive gca effect. The estimates of sca effect indicated that none of the hybrids exhibited significant positive sca effect for panicle length. Hence, no cross combination could be considered a superior specific combiner for panicle length based on sca effect. These results are in accordance with the results reported by Aruna *et al.* (2024) Balasubramanian and Vennila (2024) [5, 6] for sca effect and Kalyar *et al.* (2024) [6] for gca effect.

Higher number of grains per panicle is a desirable trait in rice as it contributes directly to grain yield. The estimates of gca effect revealed that among the lines, IET-31950 (7.78) exhibited a significant positive gca effect and was identified as a good general combiner for improving grains per panicle. Among the testers, GR-23 (16.38), GNR-9 (14.75) and IET-31937 (15.28) recorded significant positive gca effect and were recognized as good general combiners for this trait. With respect to sca effect, the cross IET-31950 × GR-23 (35.54) recorded the highly significant positive sca effect. These results are supported by Bhatti *et al.* (2015), Krishna *et al.* (2018), Garkoti and Pandey (2022) and Neupane (2022) [7, 11, 19].

Grain yield per plant is the most important economic trait. The estimates of gca effects revealed that among the lines, DRR DHAN-48 (3.66) exhibited a significant positive gca effect and was identified as a good general combiner for grain yield per plant.

Among the testers, IET-31929 (3.38) recorded a significant positive gca effect and was therefore considered a good general combiner for this trait. The sca effect of crosses revealed that three hybrids exhibited highly significant positive sca effect for grain yield per plant. The cross DRR DHAN-48 × DRR DHAN-45 (8.60) recorded the highest significant positive sca effect. This hybrid was identified as superior cross combination for grain yield per plant and may be exploited further for the development of high-yielding rice hybrids. The present study is in agreement with the results of Bhatti *et al.* (2015), Krishna *et al.* (2018), Garkoti and Pandey (2022), Balasubramanian and Vennila (2024) and Kalyar *et al.* (2024) [6, 7, 11, 19].

For straw yield per plant, positive gca and sca effects are desirable. The estimates of gca effect revealed that among the lines, IET-31950 (2.36) exhibited a significant positive gca effect and was identified as a good general combiner for straw yield per plant. Among the testers, IET-31937 (6.93) and GR-23 (4.01) recorded significant positive gca effect and were identified as good general combiners for this trait. The estimates of sca effect indicated that five crosses exhibited significant positive sca effect for straw yield per plant. The cross IET-31950 × GR-23 (21.12) recorded the highest significant positive sca effect and identified as the most promising cross combination owing to its high and significant positive sca effect. The present study is in agreement with the findings of Prajapati (2016), Vadivel (2018), Dianga *et al.* (2020), Garkoti and Pandey (2022), Maring (2023) and Ali *et al.* (2025) [1, 9, 11, 22, 26, 30].

For harvest index, positive gca and sca effects are desirable as they indicate greater partitioning of assimilates towards economic yield. The estimates of gca effect revealed that among the lines, DRR DHAN-48 (4.01) exhibited a significant positive gca effect and was identified as a good general combiner for this trait. Among the testers, GR-26 (1.75) exhibited positive gca effect; however, the effect was non-significant. The estimates of sca effect revealed that three hybrids exhibited significant sca effect for harvest index in desirable direction. The crosses, IET-31950 × IET-31929 (4.83) recorded highest significant positive sca effect and was identified as superior cross combination for improving harvest index. These results are in confirmation with the findings of Bhatti *et al.* (2015), Prajapati (2016), Kargbo *et al.* (2019), Dianga *et al.* (2020), Yadav *et al.* (2021), Kalyar *et al.* (2024) and Ali *et al.* (2025) [1, 7, 9, 16, 17, 26, 33].

Table 2: General combining ability effects of parents for different characters

Parents	Days to 50 % flowering	Plant height	Productive tillers pre plant	Panicle length	Grains per panicle	Grain yield per plant	Straw yield per plant
LINES							
DRR DHAN-48	-0.25	-4.39	0.83**	-0.34	-4.13**	3.66**	-3.89**
NVSR-6640	1.20	1.57	-0.14	0.29	-3.65*	-0.63	1.53
IET-31950	-0.96	2.82	-0.68**	0.04	7.78**	-3.02**	2.36*
SE (gi)	0.68	2.30	0.09	0.41	1.38	0.56	1.04
TESTER							
GR-15	2.25	-7.34	-0.56**	-0.72	-21.58**	-3.05**	-4.12*
GR-23	2.25	3.10	0.29	-0.47	16.38**	1.82	4.01*
GR-26	2.36*	1.61	-0.26	1.22	-0.48	-1.07	-5.12**
GNR-9	0.14	3.23	0.02	0.88	14.75**	1.34	-0.36
DRR DHAN-45	0.47	-0.81	0.28	-0.06	-6.21*	0.70	0.81
IET-31937	-4.64**	0.83	-0.12	0.30	15.28**	0.12	6.93**
IET-31929	0.14	-0.17	0.87**	0.18	2.20	3.38**	2.66
IET-31938	-2.97*	-0.46	-0.51*	-1.33	-20.35**	-3.25**	-4.81**
SE(gj)	1.12	3.77	0.16	0.67	2.26	0.91	1.70

Table 2: Conti…

Parents	Harvest index	Kernel length	Kernel breadth	L/B ratio	100 grains weight	Protein content	Amylose content
LINES							
DRR DHAN-48	4.01**	-0.11*	-0.06**	0.03	-0.16**	1.90**	-0.40
NVSR-6640	-1.10	-0.11*	0.00	-0.06	-0.00	-1.36**	-0.35
IET-31950	-2.91**	0.22**	0.05**	0.02	0.16**	-0.54**	0.76**
SE (gi)	0.65	0.05	0.02	0.03	0.03	0.04	0.27
TESTER							
GR-15	-0.53	-0.02	0.04	-0.10	0.15**	-0.46**	-0.47
GR-23	0.30	-0.06	-0.06*	0.10	-0.14**	0.05	-0.18
GR-26	1.75	-0.10	-0.16**	0.18**	0.05	-0.32**	-0.41
GNR-9	0.54	-0.06	-0.06*	0.08	-0.08	0.81**	1.68**
DRR DHAN-45	-0.22	0.19*	0.03	0.04	0.13*	0.59**	0.00
IET-31937	-2.75*	0.13	0.05	-0.02	-0.10	-0.17*	-0.41
IET-31929	0.97	-0.05	0.09**	-0.17*	-0.18**	-0.15*	0.77
IET-31938	-0.05	-0.01	0.08*	-0.11	0.17**	-0.35**	-0.97*
SE(gj)	1.07	0.08	0.03	0.06	0.05	0.07	0.45

* and ** indicates significance at 5 % and 1 % levels of probability, respectively

For kernel length, gca and sca effects are desirable in positive direction. The estimates of gca effect revealed that among the lines, IET-31950 (0.22) exhibited a significant positive gca effect and was identified as a good general combiner for kernel length. Among the testers, DRR DHAN-45 (0.19) exhibited a significant positive gca effect and was therefore identified as a good general combiner for this trait. The estimates of sca effect indicated that eight crosses exhibited significant sca effect for kernel length. Among them, IET-31950 × GR-26 (0.57) recorded the highest significant positive sca effect. This is in agreement with the results of Nanditha *et al.* (2021), Garkoti and Pandey (2022), Manivelan *et al.* (2022) and Santhiya *et al.* (2024) [11, 23, 27].

For kernel breadth, positive gca and sca effects are desirable for increasing grain width. The estimates of gca effect revealed that among the lines, IET-31950 (0.05) exhibited a significant positive gca effect and was identified as a good general combiner for kernel breadth. Among the testers, IET-31929 (0.09) and IET-31938 (0.08) recorded positive gca effect and were identified as good general combiners for this trait. The estimates of sca effect indicated that three crosses exhibited significant positive sca effect for kernel breadth. The cross IET-31950 × GR-23 (0.18) recorded the highest significant positive sca effect. Similar results were found by Saravanan *et al.* (2018), Vadivel (2018), Dianga *et al.* (2020), Nanditha *et al.* (2021), Garkoti and Pandey (2022), Manivelan *et al.* (2022), Maring (2023) and Santhiya *et al.* (2024) [9, 11, 22, 23, 27, 28, 30].

For L/B ratio, positive gca and sca effects are desirable as they indicate slender grain shape and better grain quality. The estimates of gca effect revealed that none of the lines exhibited significant gca effect for this trait. Among the testers, GR-26 (0.18) exhibited a significant positive gca effect and was identified as a good general combiner for L/B ratio. The estimates of sca effect indicated that two crosses exhibited significant positive sca effect for L/B ratio. The cross NVSR-6640 × GR-23 (0.40) recorded the highest significant positive sca effect. Present results are in close agreement with earlier reports by Vadivel (2018), Saravanan *et al.* (2018), Kargbo *et al.* (2019), Nanditha *et al.* (2021) and Manivelan *et al.* (2022) [17, 21, 23, 28, 30].

For 100 grain weight, positive gca and sca effects are desirable as they contribute directly to increased grain weight and overall yield. The estimates of gca effect revealed that among the lines, IET-31950 (0.16) exhibited a significant positive gca effect and was identified as a good general combiner for this trait. Among the testers, GR-15 (0.15), DRR DHAN-45 (0.13) and IET-31938 (0.17) exhibited significant positive gca effects and were identified as good general combiners for improving 100 grain weight. The estimates of sca effect indicated that four crosses exhibited significant positive sca effect for 100 grain weight. The cross DRR DHAN-48 × GR-23 (0.35) recorded the highest significant positive sca effect and was identified as superior specific combiner for improving 100 grain weight. Krishna *et al.* (2018), Saravanan *et al.* (2018), Vadivel (2018), Nanditha *et al.* (2021), Yadav *et al.* (2021) [19, 23, 28, 30, 33], Dodake *et al.* (2022), Garkoti and Pandey (2022), Kushal *et al.* (2023), Maring (2023), Aruna *et al.* (2024), Balasubramanian and Vennila (2024), Ali *et al.* (2025) and Talha *et al.* (2026) [1, 5, 6, 11, 20, 22, 29] reported similar results for this trait.

For protein content, positive gca and sca effects are desirable as they contribute to improved nutritional quality of rice grains. The estimates of gca effects revealed that among the lines, DRR DHAN-48 (1.90) exhibited a significant positive gca effect and was identified as a good general combiner for improving protein content. Among the testers, GNR-9 (0.81) and DRR DHAN-45 (0.59) recorded significant positive gca effect and were therefore recognized as good general combiners for this trait. The estimates of sca effect revealed that several crosses exhibited significant positive sca effect for protein content. Among them, IET-31950 × DRR DHAN-45 (1.17) recorded the highest significant positive sca effect and was identified as superior cross combinations for improving protein content. These results are in accordance with the results reported by Prajapati (2016), Dianga *et al.* (2020), Maring (2023) and Kalyar *et al.* (2024) [9, 16, 22, 26].

With regard to gca effect of parents for amylose content, among the lines, IET-31950 (0.76) exhibited a significant positive gca effect and was identified as a good general combiner for this trait. Among the testers, GNR-9 (1.68) exhibited a significant positive gca effect. The estimates of sca effect revealed that two crosses exhibited significant positive sca effects for amylose content. The hybrid IET-31950 × IET-31929 (1.91) recorded the highest significant positive sca effect followed by DRR DHAN-48 × GR-15 (1.64). Present results are in close agreement with earlier reports of several workers like Manivelan *et al.* (2022) and Maring *et al.* (2023) [21, 22].

The heatmap in Figure 1, provides a visual representation of the general combining ability (GCA) effects of the parental genotypes across all yield and quality traits studied. Considerable variation in GCA effects was observed among the parents, indicating differential genetic potential for trait improvement. Parents such as DRR DHAN-48, IET-31950, IET-31929 and GNR-9 exhibited desirable GCA effects for several economically important traits, suggesting their usefulness as superior donors in hybridization programmes.

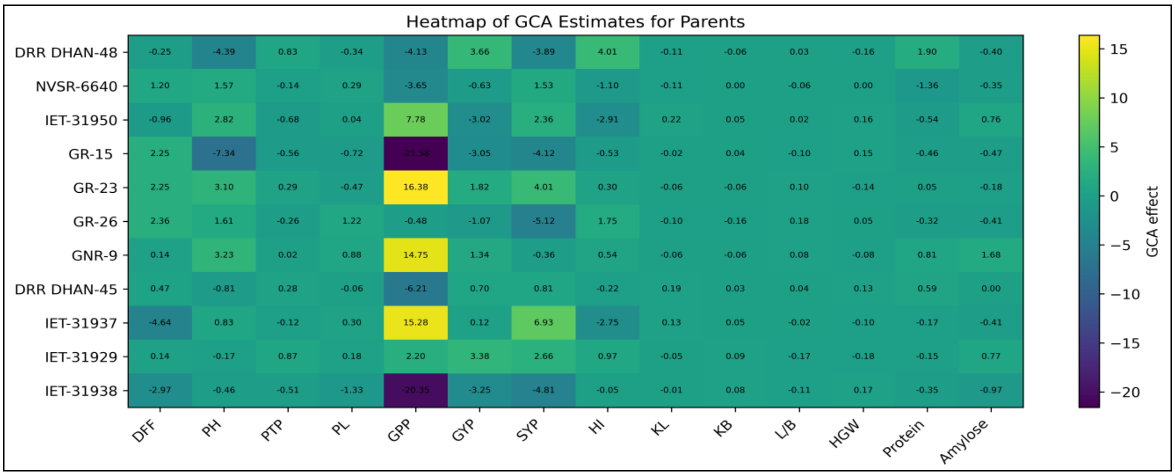

Fig 1: Heatmap representing the general combining ability (GCA) effects of 11 parental genotypes for 14 yield and quality traits in rice (*Oryza sativa* L.). The color gradient indicates the magnitude and direction of GCA effects, where contrasting colors represent positive and negative combining ability effects for the respective traits.

The ratio of GCA variance to SCA variance ($\sigma^2_{gca}/\sigma^2_{sca}$) was found to be less than unity for days to 50 per cent flowering (0.22), productive tillers per plant (0.43), grains per panicle (0.23), grain yield per plant (0.34), straw yield per plant (0.09), harvest index (0.98), kernel length (0.17), kernel breadth (0.14), kernel L/B ratio (0.12), 100 grain weight (0.52) and amylose content (0.22) indicating the predominance of non-additive gene action in the inheritance of these traits. Plant height (-0.87) and panicle length (-0.03) also exhibited predominance of non-additive gene action as the estimates of SCA variance were higher than the corresponding GCA variance. In contrast, protein content recorded a $\sigma^2_{gca}/\sigma^2_{sca}$ ratio greater than unity (4.17) indicating the predominance of additive gene action governing this trait. Therefore, non-additive gene action was predominant for most of the characters studied, whereas additive gene action played a major role in the inheritance of protein content.

For each character the additive and dominance variances were estimated. Protein content exhibited additive variance greater than dominance variance (V_A = 8.64; V_D = 2.07), suggesting that this trait may respond effectively to selection due to the predominance of additive gene action.

All the remaining traits *viz*., days to 50 per cent flowering, plant height, productive tillers per plant, panicle length, grains per panicle, grain yield per plant, straw yield per plant, harvest index, kernel length, kernel breadth, kernel L/B ratio, 100 grain weight and amylose content exhibited higher dominance variance than additive variance, indicating the predominance of non-additive gene action. Hence, improvement of these characters could be achieved more effectively through heterosis breeding and exploitation of hybrid vigour. The estimates of general combining ability (gca) effects of parents and specific combining ability (sca) effects of hybrids for 14 traits are presented in Table 2 and 3, respectively.

Among the lines, DRR DHAN-48 was identified as a good general combiner for productive tillers per plant, grain yield per plant, harvest index and protein content, whereas IET-31950 exhibited desirable gca effects for number of grains per panicle, straw yield per plant, kernel length, kernel breadth, 100 grain weight and amylose content.

Among the testers, IET-31929 was found to be a good general combiner for productive tillers per plant, grain yield per plant and kernel breadth. Similarly, GNR-9 was a good general combiner for number of grains per panicle, protein content and amylose content, whereas IET-31937 exhibited desirable gca effects for days to 50 per cent flowering, number of grains per panicle and straw yield per plant. In addition, GR-23 was identified as a good general combiner for number of grains per panicle, straw yield per plant and GR-15 for 100 grains weight.

Furthermore, it was found that parents possessing various general combining abilities for the same trait displayed differences in their offspring, proving that each male and female line has a unique genetic makeup and the capacity to pass on its traits to offspring.

The estimates of sca effect (Table 3) revealed that none of the hybrids was consistently superior for all the characters studied. However, DRR DHAN-48 × DRR DHAN-45 expressed desirable and significant sca effect for productive tillers per plant (1.93), number of grains per panicle (26.90), grain yield per plant (8.60) and straw yield per plant (18.37). Likewise, IET-31950 × GR-23 exhibited favourable and significant sca effect for productive tillers per plant (1.29), number of grains per panicle (35.54), grain yield per plant (5.27) and straw yield per plant (21.12). The cross NVSR-6640 × IET-31929 showed desirable significant sca effects for number of grains per panicle (28.86), straw yield per plant (9.88), kernel length (0.46) and protein content (0.77). Among the quality traits, IET-31950 × GR-26 was identified as a superior specific combiner for kernel length (0.57), while IET-31950 × GNR-9 (1.10), NVSR-6640 × IET-31929 (0.77), DRR DHAN-48 × IET-31938 (0.44), NVSR-6640 × IET-31937 (0.38), DRR DHAN-48 × GR-15 (0.36) and NVSR-6640 × GR-26 (0.26) exhibited desirable significant sca effects for protein content. These hybrids may therefore be exploited further for the development of high yielding and superior quality rice genotypes.

The heatmap in Figure 2, provides a comprehensive visualization of the variation in specific combining ability (SCA), effects among the 24 F_1 hybrids for the studied yield and quality traits. Considerable differences in SCA effects were observed, reflecting the predominance of non-additive gene action for most traits. Hybrids such as DRR DHAN-48 × DRR DHAN-45, IET-31950 × GR-23, and NVSR-6640 × IET-31929 exhibited desirable SCA effects for several important traits, indicating their potential as promising hybrid combinations for improving grain yield and quality.

Table 3: Specific combining ability effects of crosses for different characters

CROSSES	Days to 50 % flowering	Plant height	Productive tillers per plant	Panicle length	Grains per panicle	Grain yield per plant	Straw yield per plant
DRR DHAN-48 × GR-15	2.25	3.66	-0.65*	1.16	12.00**	-1.77	5.69
DRR DHAN-48 × GR-23	-3.75	-1.24	-1.75**	0.58	-25.16**	-6.98**	-13.92**
DRR DHAN-48 × GR-26	1.80	-0.17	-0.25	-0.61	-0.43	-1.38	0.05
DRR DHAN-48 × GNR-9	1.36	2.60	1.36**	0.41	-6.93	5.82**	0.32
DRR DHAN-48 × DRR DHAN-45	4.02*	-9.73	1.93**	-0.29	26.90**	8.60**	18.37**
DRR DHAN-48 × IET-31937	-2.1	6.22	-0.30	-0.85	-11.56**	-2.38	-8.47**
DRR DHAN-48 × IET-31929	0.36	2.42	0.30	-0.34	-7.55	-1.24	-0.09
DRR DHAN-48 × IET-31938	-3.86	-3.77	-0.63	-0.05	12.74**	-0.64	-1.95
NVSR-6640 × GR-15	1.12	-0.77	0.12	-1.34	2.68	0.46	1.50
NVSR-6640 × GR-23	1.79	-3.99	0.45	-0.31	-10.38*	1.71	-7.20*
NVSR-6640 × GR- 26	1.68	-5.84	-0.17	-0.15	-9.21*	0.01	-8.56**
NVSR-6640 × GNR-9	-2.09	1.06	-0.01	-0.91	7.95*	0.42	7.10*
NVSR-6640 × DRR DHAN-45	-2.76	1.28	-0.52	0.23	-14.24**	-4.36**	-11.77**
NVSR-6640 × IET-31937	-3.31	0.35	0.24	0.57	-5.38	1.61	4.13
NVSR-6640 × IET-31929	-1.43	3.65	-0.32	1.51	28.86**	0.09	9.88**
NVSR-6640 × IET-31938	5.01*	4.25	0.21	0.40	-0.27	0.02	4.92
IET-31950 × GR-15	-3.37	-2.88	0.53	0.17	-14.68**	1.31	-7.19*
IET-31950 × GR-23	1.95	5.23	1.29**	-0.26	35.54**	5.27**	21.12**
IET-31950 × GR-26	-3.48	6.01	0.43	0.76	9.64*	1.37	8.50**
IET-31950 × GNR-9	0.73	-3.67	-1.34**	0.49	-1.01	-6.25**	-7.42*
IET-31950 × DRR DHAN-45	-1.26	8.45	-1.41**	0.05	-12.65**	-4.24*	-6.60*
IET-31950 × IET-31937	5.51**	-6.58	0.05	0.28	16.94**	0.77	4.34
IET-31950 × IET-31929	1.06	-6.08	0.02	-1.16	-21.30**	1.14	-9.78**
IET-31950 × IET-31938	-1.15	-0.48	0.42	-0.34	-12.45**	0.61	-2.97
S.E(g_{ij})	1.93	6.53	0.28	1.17	3.92	1.59	2.94

Table 3: conti…

CROSSES	Harvest index	Kernel length	Kernel breadth	L/B ratio	100 grains weight	Protein content	Amylose content
DRR DHAN-48 × GR-15	-3.51	0.20	-0.00	0.08	-0.04	0.36**	1.64*
DRR DHAN-48 × GR-23	1.53	-0.08	0.14*	-0.25*	0.35**	-0.00	-0.81
DRR DHAN-48 × GR-26	-0.80	-0.58**	-0.19**	0.03	-0.07	0.12	-0.22
DRR DHAN-48 × GNR-9	3.57	-0.41**	-0.26**	0.19	-0.16	-0.94**	-0.72
DRR DHAN-48 × DRR DHAN-45	-2.72	0.35*	0.07	0.04	-0.32**	-0.04	1.39
DRR DHAN-48 × IET-31937	1.93	0.15	0.05	0.01	0.04	0.00	1.17
DRR DHAN-48 × IET-31929	-0.96	0.14	0.04	0.02	0.20*	0.04	-3.01**
DRR DHAN-48 × IET-31938	0.97	0.22	0.15*	-0.13	0.00	0.44**	0.57
NVSR-6640 × GR-15	-0.73	-0.43**	-0.03	-0.15	-0.04	0.19	0.12
NVSR-6640 × GR-23	3.19	-0.19	-0.32**	0.40**	0.02	0.09	-0.76
NVSR-6640 × GR- 26	4.04*	0.01	0.10	-0.17	0.09	0.26*	0.65
NVSR-6640 × GNR-9	-2.37	0.17	0.17	-0.17	-0.16	-0.16	1.25
NVSR-6640 × DRR DHAN-45	2.55	0.143	-0.02	0.07	0.17*	-1.13**	-0.48
NVSR-6640 × IET-31937	-0.67	0.01	-0.08	0.10	-0.18*	0.38**	-0.81
NVSR-6640 × IET-31929	-3.87*	0.46**	0.10	0.08	0.00	0.77**	1.10
NVSR-6640 × IET-31938	-2.142	-0.17	0.08	-0.17	0.10	-0.41**	-1.07
IET-31950 × GR-15	4.24*	0.22	0.04	0.06	0.08	-0.55**	-1.76*
IET-31950 × GR-23	-4.72*	0.27	0.18**	-0.14	-0.38**	-0.08	1.58
IET-31950 × GR-26	-3.24	0.57**	0.08	0.14	-0.01	-0.38**	-0.43
IET-31950 × GNR-9	-1.19	0.23	0.08	-0.02	0.33**	1.10**	-0.53
IET-31950 × DRR DHAN-45	0.17	-0.49**	-0.04	-0.11	0.14	1.17**	-0.90
IET-31950 × IET-31937	-1.26	-0.16	0.03	-0.11	0.14	-0.39**	-0.36
IET-31950 × IET-31929	4.83*	-0.60**	-0.14*	-0.10	-0.20*	-0.82**	1.91*
IET-31950 × IET-31938	1.17	-0.05	-0.23**	0.30**	-0.10	-0.03	0.50
S.E(gij)	1.85	0.15	0.05	0.11	0.08	0.13	0.79

* and ** indicates significance at 5 % and 1 % levels of probability, respectively

Nature and magnitude of combining ability effects helps in identifying superior parents for their utilization in further breeding programme. Estimates of gca effect in the present investigation revealed that no parent was good general combiner for all traits together and as such combining ability effects of parents were not consistent for various traits. The parents classified as good, average or poor combiner for all traits is presented, in Table 4. The parents showing significant estimates of gca effect in desirable direction (positive or negative based on character) was designated as good general combiner and parents depicting significant estimates of gca effect in undesirable direction were considered as poor general combiners. Parents having non-significant gca effect (in either direction) were classified as average general combiners.

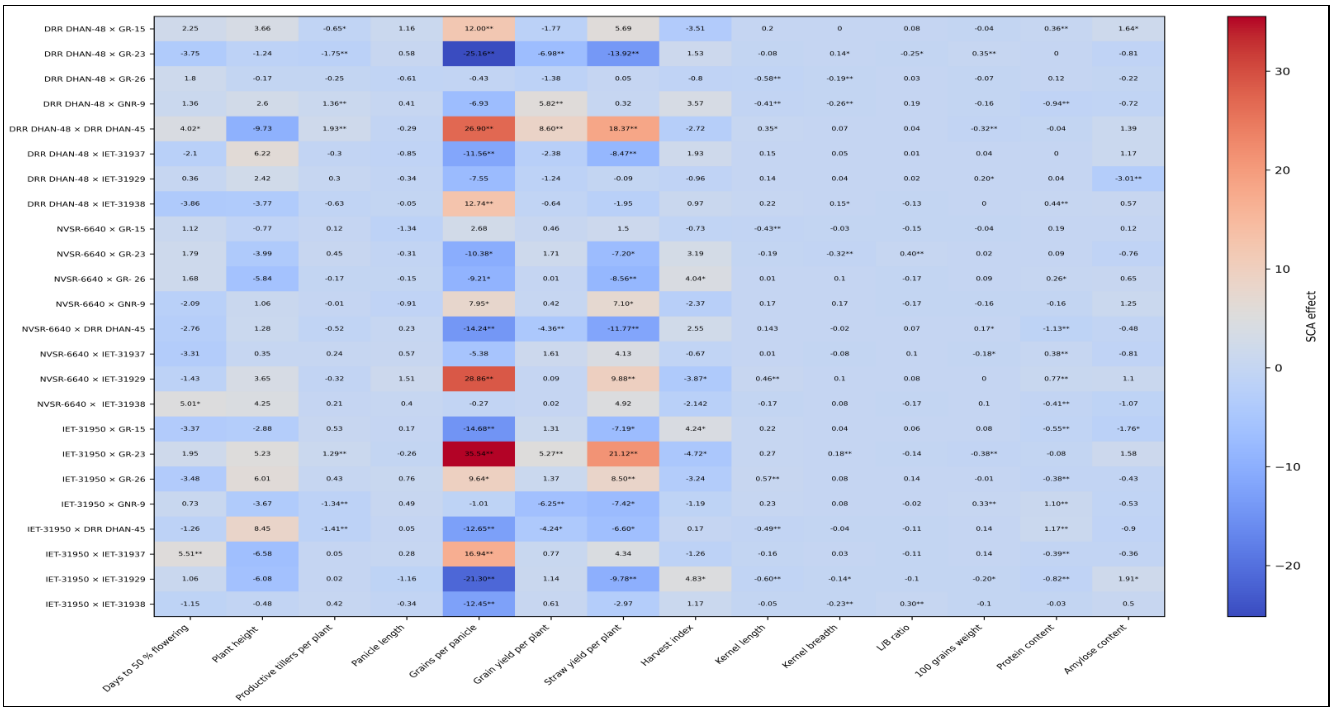

Fig 2: Heatmap of specific combining ability (SCA) effects of 24 F_1 rice hybrids for yield and quality traits. The heatmap illustrates the magnitude and direction of SCA effects across 14 quantitative and quality traits, with warmer colours indicating positive SCA effects and cooler colours indicating negative SCA effects. The numerical values within each cell represent the estimated SCA effects, while * and ** denote significance at the 5% and 1% probability levels, respectively.

The crosses exhibiting high sca effects did not always involve both parents possessing high gca effects, suggesting the importance of both intra and inter-allelic interactions in the inheritance of these traits. In most cases, high sca effects were associated with high heterotic response; however, such crosses also involved parents with average or poor gca effects. The crosses showing high sca effect for grain yield per plant generally possessed desirable sca effect for several yield contributing characters, indicating the cumulative contribution of these component traits towards higher grain yield and heterosis.

The crosses having high sca effect and superior *per se* performance with one or both parents identified as good general combiners for grain yield per plant are expected to produce desirable transgressive segregants in subsequent generations. Therefore, such cross combinations may be advanced to later segregating generations for the identification and selection of superior recombinants.

The results of the present investigation revealed that the magnitude of SCA variance was higher than GCA variance for most of the characters studied, indicating the predominance of non-additive gene action in their inheritance. This was further supported by the low values of $\sigma^2_{gca}/\sigma^2_{sca}$ ratios, which were less than unity for all the traits except protein content. Protein content exhibited a $\sigma^2_{gca}/\sigma^2_{sca}$ ratio greater than unity, indicating the predominance of additive gene action. Therefore, heterosis breeding may be effectively exploited for the improvement of grain yield and most of its yield contributing and quality traits, whereas simple selection procedures in segregating generations may be more effective for improving protein content.

Table 4: Summary of general combining ability effects of the parents for 14 characters

Parents	Days to 50 % flowering	Plant height	Productive tillers per plant	Panicle length	Grains per panicle	Grain yield per plant	Straw yield per plant
LINES							
DRR DHAN-48	A	A	G	A	P	G	P
NVSR-6640	A	A	A	A	P	A	A
IET-31950	A	A	P	A	G	P	G
TESTER							
GR-15	A	A	P	A	P	P	P
GR-23	A	A	A	A	G	A	G

GR-26	P	A	A	A	A	A	P
GNR-9	A	A	A	A	G	A	A
DRR DHAN-45	A	A	A	A	P	A	A
IET-31937	G	A	A	A	G	A	G
IET-31929	A	A	G	A	A	G	A
IET-31938	G	A	P	A	P	P	P

Table 4: conti.

Parents	Harvest index	Kernel length	Kernel breadth	L/B ratio	100 grains weight	Protein content	Amylose content
LINES							
DRR DHAN-48	G	P	P	A	P	G	A
NVSR-6640	A	P	A	A	A	P	A
IET-31950	P	G	G	A	G	P	G
TESTER							
GR-15	A	A	A	A	G	P	A
GR-23	A	A	P	A	P	A	A
GR-26	A	A	P	G	A	P	A
GNR-9	A	A	P	A	A	G	G
DRR DHAN-45	A	G	A	A	G	G	A
IET-31937	P	A	A	A	A	P	A
IET-31929	A	A	G	P	P	P	A
IET-31938	A	A	G	A	G	P	P

G = Good general combiner having significant gca effect in desired direction
A = Average general combiner having either positive or negative but non-significant effects
P = Poor general combiner having significant gca effect in undesired direction

Conclusion

Among the parents, DRR DHAN-48 was identified as a good general combiner for productive tillers per plant, grain yield per plant, harvest index and protein content, while IET-31950 was found to be a good general combiner for grains per panicle, straw yield per plant, kernel length, kernel breadth, 100 grain weight and amylose content. Among the testers, GNR-9 emerged as a desirable general combiner for grains per panicle, protein content and amylose content, whereas IET-31929 was identified as a good general combiner for productive tillers per plant, grain yield per plant and kernel breadth. These parents may therefore be utilized effectively in future breeding programmes. The study on specific combining ability effects indicated that the hybrids DRR DHAN-48 × DRR DHAN-45, DRR DHAN-48 × GNR-9 and IET-31950 × GR-23 were highly promising for grain yield and several yield contributing characters.

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